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INTERRELATIONSHIPS OF THE SPOROZOA.

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OTHER things being equal, it is perhaps an easier task to determine the interrelationships of a group of parasites than those of a series of free-living forms. Once the parasitic habit is acquired, development is confined within narrow limits. Two definite lines are followed. These are: morphological degradation, and complication of the life history combined with increased fecundity. It is perfectly evident why this should be. Individually, the parasite is at once relieved of two of the great problems of animal existence. These are: the obtaining of food and the avoidance of serving as food for some other animal. The parasite has no enemies and abundant food surrounds it on all sides. As a result, various parts necessary to a free-living animal are lost. These are: the organs concerned with the capture and digestion of food, and those which serve as protection against the attacks of enemies. On the other hand, the new mode of life involves new needs, and the organism responds by the production of new organs. Such are: hooks, providing for the maintenance of a fixed position, and, in many cases, beaks or rostra which enable their possessors to bore through the tissues of the host.

Finally, a parasite acquires the ability to resist being digested. This appears in some cases to result from the formation of a differentiated external layer, but in general it is to be credited to some property of the living protoplasm. It is, necessarily, a property possessed by all organisms which live within others, and hence has no taxonomic value.

But if the existence of the individual is rendered easier, that of the species is menaced by a danger not experienced by free-living forms. With these, birth, growth, and reproduction all take place in free nature. For the most part, the eggs and young are left to shift for themselves, but the dangers which they encounter, are much the same as those which threaten the adults. The greater mortality during these stages is primarily due to their greater helplessness. But it is far different in the case of parasites. For these the course must, so to speak, consist of a series of leaps. A given host, at best, eventually dies and its death involves that of its parasites, as individuals. Hence the eggs or spores must be transferred to another host or else the species will cease to exist. Parasites are so abundant, and so thoroughly well established that we are prone to overlook what a radical departure this is from the ordinary scheme of animal life. The elements destined to tide the species over this critical period reach the exterior in one of several ways. The more usual are either by the death of the host, or by being carried out with its fæces. Ordinarily animals do not eat either their own dead or their own fæces, whence the only chance the germ has is to become attached to the food and so swallowed. Accordingly, as a general rule, parasites are common in social and uncommon in solitary animals. The termites, which do eat their fæces, invariably have their intestines literally packed with the curious *Trichonymphidæ*.

The response of the species to this acquired peril is two-fold. Complications are introduced into the life history. These are of such a character as to increase the probability of obtaining lodgment within the appropriate host. This is the most striking feature displayed by parasites. The other response is the acquisition of great fecundity. Great stress is always laid upon this, yet it is after all doubtful if parasites, taken as a whole, do

actually exceed other less specialized forms of life in their reproductive powers. Nevertheless the germs are produced in such numbers that if one in many thousands survive, the perpetuation of the line is assured.

Examples in support of the statements given above are numerous. Certain animals, particularly the small Nematodes, live indifferently either in the outside world or else upon or within higher forms. Such may be regarded as upon the threshold of the parasitic life. A second step is taken by those Flagellates which inhabit the recta of frogs and salamanders. These animals are morphologically like their free-living congeners nor is their life history known to be more complicated. But turning to the flat-worms we find the parasitic habit in its most confirmed aspect. This phylum, moreover, furnishes us with a series of stages from typical free-living forms to typical parasites. It is divided into three classes: the Turbellaria, the Trematoda, and the Cestoda. The first class consists mainly of free-living animals, and is characterized by an alimentary canal and a ciliated epidermis. The Trematoda retain the intestine, but have lost the cilia. The Cestodes go farther, and losing all trace of an alimentary canal, absorb their nutriment through the epidermis. There is thus a progressive morphological degradation.

But along with this change in the individual, there is a striking change in the life history. In the free-living Turbellaria and the ectoparasitic Trematodes, development is direct. That is, the eggs produce young which grow to be adults without metamorphosis. On the other hand, the endoparasitic Trematodes and the Cestodes bear off the palm for a complicated life history. The organisms hatched from the eggs are wholly unlike the adults, and there is always at least one metamorphosis. In addition, change of host is invariable. Thus, the liver fluke of the sheep spends a part of its existence in a water snail. Indeed, from a purely utilitarian standpoint, these animals appear to have overshot the mark, and their ontogenetic development defies a rational explanation. The desired end could apparently have been reached quite as certainly by less devious methods. But while we cannot explain the *raison d'être* for such processes, it is evident that they indicate a confirmed parasitism. These

animals are without doubt the descendants of a long line of parasitic ancestors and they probably represent the limit to which the habit can go.

We are thus furnished with two criteria enabling us to gauge the modifications induced by this mode of life. That is, given two allied groups of parasites, that possessing the more degraded organization and more complex life history is to be considered as the less primitive. A third criterion is furnished by the part of the host chosen for a habitat. Without doubt, the original gateway was the mouth or the rectum. Thus the less modified parasites are inhabitants of the alimentary canal. Examples are such animals as *Amœba blattæ* and the various Flagellates mentioned above, which dwell in the recta of frogs and salamanders. Access to the lungs and liver is also easy, although some of the parasites of the latter organ reach their chosen place by an indirect path. In the case of the inhabitants of the sexual organs, muscles, and brain, the infection comes in most cases by way of the intestine. There is, however, no direct road and the parasite must bore its way through the tissues of the host. These parasites are generally of the most modified types. On the contrary, the greatly modified Cestodes, at least in one of their hosts, live in the alimentary canal. This criterion, then, needs to be used with much more caution than the other two.

Having obtained certain criteria, I shall endeavor to apply them to the matter in hand, as indicated by the title of my communication. The Sporozoa stand alone. Their ancestors were in all probability Protozoan, but they branched off at so early a period that there remain absolutely no connecting links between them and any of the other classes of the Protozoa. There are two rival views regarding their origin. Minchin¹ aptly terms these the euglenoid and the amœboid hypotheses. The one regards the Flagellates, the latter the Rhizopods, as the ancestral forms. Bütschli has advocated the former, whereas Minchin pronounces in favor of the latter. To me, however, it appears that neither can be adopted without reserve. Each, by implication, assumes that all Sporozoa have had a common

¹ *A Treatise on Zoölogy*, edited by E. Ray Lankester, Chapter I, Section K.

origin, which, for reasons that I shall give, does not appear to be the case.

The class itself falls readily into two subclasses: the Telosporidia and the Neosporidia. In the former, arrived at a certain stage of its existence, the individual divides into reproductive elements, the spores, and ceases to exist as an individual. In the latter, vegetative growth and spore formation proceed hand in hand. Further, the Telosporidia display sexual differentiation of fully as definite a character as the mammals, while nothing of the sort has as yet been described for the Neosporidia.

The division into lesser groups is as follows:—

TELOSPORIDIA.

Order 1, *Gregarinida*.

Suborder 1, Schizogregarinæ.

Suborder 2, Eugregarinæ.

Tribe 1, Acephalina [Monocystidea].

Tribe 2, Cephalina [Polycystidea].

Order 2, *Coccidia*.

Order 3, *Hæmosporidia*.

Suborder 1, Hæmosporea.

Suborder 2, Acystosporea.

NEOSPORIDIA.

Order 1, *Myxosporidia*.

Suborder 1, Phænocystes.

Suborder 2, Cryptocystes.

Order 2, *Sarcosporidia*.

Order 3, *Haplosporidia*.

This is Minchin's classification, excepting the fact that I have included the Haplosporidia. Doflein¹ rates the Coccidia and Hæmosporidia as suborders, the two making up the order Coccidiomorpha. This is probably an improvement.

¹ *Archiv für Protistenkunde*, vol. 1, 1902.

Of all the Telosporidia, the Polycystidea stand highest in organization. Their name indicates the fact that they are divided into parts. The division is longitudinal and the parts, from before backward, are termed epimerite, protomerite, and deutomerite. The epimerite is an organ of attachment, comparable to the suckers of Trematodes and the hooks of Cestodes. It is peculiar to the Polycystidea and has evidently been evolved to meet the requirements of an intestinal life. The protomerite and deutomerite are the two "cysts" of the gregarine body. The latter is nearly always much the larger, and contains the nucleus.

From without inward, the ectosarc of a Polycystid gregarine shows epicyte, sarcocyte, and myocyte. The epicyte is a membrane of some formed substance. Its function is probably to guard against the too rapid action of the fluids of the host's intestine. The sarcocyte in protoplasmic and an ingrowth from it forms the septum which separates the protomerite from the deutomerite. The myocyte is a muscular system of longitudinal and transverse fibers. By means of various contractions of these fibers gregarines are able to change shape and to display locomotor movements.

It is thus seen that as regards both form and anatomy the Polycystids are somewhat complicated animals. They are also exclusively intestinal parasites and there is neither change of hosts nor alternation of generations. If then our criteria be of any value, the Polycystid gregarines are the least modified of the Telosporidia and stand nearest to the stem from which the entire subclass originated. Assuming this as a working hypothesis, it remains to be seen if the remainder of the Telosporidia can be derived from them.

Gregarines develop from a minute protoplasmic body, known as a sporozoite. The sporozoite is piriform or vermiform. At the anterior end, the protoplasm is stiffened and forms the so called rostrum, by means of which the organism is able to work its way into an epithelial cell of the host's intestine. As a rule, penetration is only partial and the Polycystidea, with the exception of a single family (the Stenophoridæ), are never cell parasites. In its chosen place, the sporozoite grows to be an adult

gregarine, or trophozoite. In most cases, the attachment to the host epithelium is sooner or later lost and the gregarine takes up a free life in the intestine of its host. In some species the attachment is maintained until the animals are sexually mature, but the distinction is not important.

Although lacking in secondary sexual characters, the adult gregarines are male and female. We owe this knowledge to the recent brilliant work of Léger. At the proper period, two of opposite sex come together, conjugate, and form a cyst. Within the cyst, the male gregarine produces motile, tailed elements, the spermatozooids. The female gregarine produces rounded cells, the eggs. At maturity, the spermatozooids seek and fertilize the eggs. Each fertilized egg eventually produces a spore, the contents of which septate into eight sporozoites. Ordinarily, the cysts reach the exterior shortly after their formation, and sporulation takes place while the cyst is lying on the earth. It may, however, be completed with the cyst still in the host intestine, but auto-infection has never been described.

Eventually the cyst opens and the spores are set free. These, if they reach the intestine of another individual of the host species, dehisce and release the sporozoites. Otherwise their fate is doubtless death.

In the classification given above, the Gregarinida are ranked as an order. This order is divided into two suborders: the Schizogregarinæ and the Eugregarinæ. The former includes those animals originally termed the Amœbosporidia. They possess a fixed body form, but their anatomy is much simpler than that of the Eugregarinæ. There is an alternation of generations. So far, however, but four or five species are known, and this rarity appears to be actual and not merely the result of insufficient study. For the time being, it appears best to regard them merely as a small offshoot from the Eugregarinæ.

The Eugregarinæ are divided into tribes. In the more recent general works, these are named the Cephalina and the Acephalina. There does not seem, however, to be any good reason for abandoning the older terms Polycystidea and Monocystidea. Except for the interpolation of the Schizogregarines, this classification is the same as that which has been in vogue for many years.

Its implication is that the relationship between the Polycystidea and Monocystidea is very close. Relatively, this is true, yet there are considerable differences. For one thing, reproduction in the Monocystids is isogamous. The encysted trophozoites each break up into gametes, which are all alike. These gametes fuse in pairs to form the zygotes. It is assumed that in each zygote, one gamete has been derived from one trophozoite and the other from the other, but the point is necessarily almost impossible to demonstrate. Each zygote produces a spore.

In the second place, the Monocystidea are far simpler in organization than the Polycystidea. While some of them possess a definite body form, many do not. Moreover, as their name indicates, their bodies are never divided into two chambers, a result of the loss of the sarcocyte. It is on this same account, in all probability, that they are polymorphic. Now, throughout the Polycystidea a perfect series can be established based on the development of the sarcocyte. In some it is always thick and continuous all over the body. In others it is but feebly developed, while in a certain number the septum disappears, and these species simulate the Monocystidea. The element is obviously in a transitional state, and since we are dealing with parasites, we are warranted in supposing it is disappearing.

Considering next the life history, the Monocystids, like the Polycystids, develop from a sporozoite which is released in the intestine of the host. But whereas in the latter group the sporozoite never gets farther than the intestinal epithelium, in the former it penetrates the cœlome. Some Monocystids develop in the connective tissue surrounding the intestines of their hosts, whereas others go farther. Thus, in the Monocystids of the earthworm, the sporozoites gain the seminal vesicles before developing into gregarines.

We are thus furnished with certain data enabling us to determine which of these two groups is ancestral. The evidence awards this distinction to the Polycystidea. That furnished by the sarcocyte is very suggestive, and the Monocystidea, which lack it, are to be considered the derived group. The life history points in the same direction. It is to be assumed here, as it is in the case of most animals, that ontogeny recapitulates phy-

logeny. That is, the Monocystids have arisen from certain sporozoites, which have pushed their way entirely through the intestinal epithelium instead of remaining either attached to it or within it. Finding in this way a congenial environment, they have survived and eventually established a new group of animals.

It is thus possible to decide which of the two modes of reproduction displayed by these two groups is the more primitive. On *a priori* grounds, heterogamy can be derived from isogamy or isogamy from heterogamy. But, presumably, the more primitive group will display the more primitive mode of reproduction. Whence the conclusion appears justifiable that the lack of sexual differentiation in the Monocystidea is the result of a loss. This conclusion is supported by the fact that, in the other Telosporidia, the organisms are male and female.

The life history of a Coccidian begins in precisely the same way as that of a gregarine. A sporozoite, released in the lumen of the intestine, seeks and penetrates an epithelium cell. From this point, one of two courses may be followed. Easily satisfied, the sporozoite may settle down at once within the cell it has entered, and proceed to grow. Or else it may completely pass through the intestinal wall, and eventually come to rest within a cell of the liver, kidney, or testis. In either case, once established, the organism grows until it reaches a certain definitive size. Then, by a process termed schizogony, it divides into a number of merozoites. These seek fresh cells, which they invade. The schizogonous cycle, which may be repeated many times, occasionally produces the parasites in such numbers that the host is killed. But whether or not, at the end of a certain time, the merozoites develop into male and female cells. Each male cell produces a number of minute elements, the microgametes. Each female cell develops into a single egg, or macrogamete. At maturity, the mobile microgametes seek and fertilize the eggs. Immediately after fertilization, the egg lays down a protective covering and becomes an oöcyst.

The process differs from that in the Polycystidea in two respects. In these, the female trophozoite produces numerous eggs and fertilization takes place within the cyst. In the Coccidia, each female trophozoite metamorphoses into a single egg,

and encystment follows fertilization. The attempts to homologize these two methods are not wholly satisfactory, and do not shed much light on the relationship of the two groups. It may be observed, however, that wherein the *Coccidia* differ from the gregarines, they approach the conditions found in the highest animals.

Accordingly, in the attempt to derive the *Coccidia* from the gregarines, it is advisable to seek evidence other than that furnished by the reproductive processes. This is furnished by the life history and the habitat. The *Coccidia* display an alternation of generations and live within cells. These are both indicative of a greater specialization than is shown by the gregarines. We may imagine that in evolution certain sporozoites penetrated completely within the cells of the intestinal epithelium, and there remained and developed. Such a habit, once acquired, would speedily lead to morphological degradation. The Polycystidea may almost be said to lead a free life. They possess and exert the power to move from place to place. But the *Coccidia*, living within cells, add to the degradation which follows from a parasitic, that which results from a sedentary habit. Two influences are thus at work upon them, and they have become the most simply organized of all the Sporozoa. Their form is spherical or ellipsoidal, that taken by any non-living liquid when in a state of equilibrium. Anatomically, they are merely nucleated masses of cytoplasm, not even displaying differentiation into ectosarc and endosarc.

It then seems justifiable to derive the *Coccidia* from the Polycystidia, although perhaps indirectly, for reasons which I shall give. The fact that some inhabit the internal organs of the host presents no difficulty. In numbers, those infesting the intestinal epithelium are much in excess. These were doubtless first evolved. The intracellular habit once acquired, the organ-infesting *Coccidia* could easily have arisen from those living in the intestinal epithelium. The more venturesome sporozoites, by passing entirely through the intestinal wall, finally gained one of the internal organs. The pabulum furnished by a kidney or testis cell being satisfactory, the line was established.

The last group of the Telosporidia is the Hæmosporidia.

This order is, in some respects, the best studied of all the Sporozoa, since it numbers amongst its members the parasites of malaria and yellow fever. In the acquisition of two hosts, it reaches a higher degree of specialization than the Coccidia, and extreme specialization is also indicated by the relative paucity in species. It is to be remembered, however, that from the biological side, the group is not so well known as either the Coccidia or the Gregarinida. Accordingly, generalizations valid to-day may need to be modified as our knowledge increases.

Two suborders have been established, the Hæmosporea and the Acystosporea. With the exception of one important feature, the life history of these two is the same. It is further essentially the same as that of the Coccidia.

As in the rest of the Telosporidia, the Hæmosporidian begins its career as a sporozoite. Set free in the blood of the host, this sporozoite attacks and enters a blood cell, preferably an erythrocyte. Here it grows into a trophozoite, which is amœboid in the Acystosporea and generally vermiform in the Hæmosporea. The trophozoite, growing at the expense of the blood cell, soon breaks up into a number of merozoites. By the disintegration of the blood cell, the merozoites fall into the blood stream. Forthwith they attack new blood cells and the process (schizogony) is repeated. The increase is therefore by geometrical ratio and as Minchin says: "It is evident that reproduction at this rate could only continue indefinitely in the *ichor* of an infinite host." Accordingly, at the end of a certain number of generations, the parasite provides for its future by the production of male and female elements.

So far the process is exactly parallel to that found in the Coccidia. In the Hæmosporidia, however, or rather in the Acystosporea, the male and female cells must be removed from the blood of the host to insure further development. This removal is effected by a blood-sucking insect (a mosquito) which takes the parasites into its alimentary canal. Here they mature, the male cells forming each a number of microgametes, the female cells each a single macrogamete or egg. The microgametes fertilize the macrogametes, which then metamorphose into elongated elements, the oökinetes. The oökinete pierces the

intestinal epithelium of the mosquito and comes to rest in the peri-intestinal tissue. There is first a period of growth, during which the element assumes a spherical form and becomes inclosed by a delicate wall. No actual cyst is developed. Eventually, the sporozoites are produced directly from the protoplasmic mass, the spore stage being omitted. Excepting for the fact that fertilization is postponed until after the removal of the parasite from the vertebrate host, that part of the Acystosporean life history which is passed in the mosquito corresponds exactly to that part of the Coccidian life history which is passed in the cyst.

The Acystosporea are parasitic in the blood of mammals and birds. Intermediate hosts are known in many cases, and they are generally assumed in the rest. The Hæmosporea, on the other hand, infest reptiles and batrachians. Intermediate hosts are not known,¹ nor can we readily believe that such forms are much preyed upon by Diptera. However greatly we may dread the mandibles of the mosquito, the Chelonia are probably indifferent to its attacks. Moreover, in the case of *Lankesterella* of the frog, it has been shown by Hintze² that sexual reproduction takes place in the blood, and that the motile zygotes so formed gain the epithelium of the intestine. Here they encyst, the cysts so formed eventually reaching the exterior by being carried out with the fæces of the host.

If the life history of *Lankesterella* may be taken as representative of that of the Hæmosporea, we find that the two sub-orders of the Hæmosporidia differ only in that the Acystosporea have acquired an intermediate host. While this is indicative of more extreme specialization, it is not difficult to imagine how it may have been brought about. The warm-blooded vertebrates have doubtless long been preyed upon by blood-sucking arthropods. The crucial point in the bringing about of this change of life on the part of the parasites was that some such blood-sucker would be unable to digest them. This would be merely a matter of chance. There was probably one time in their

¹ A case has, however, recently been described.

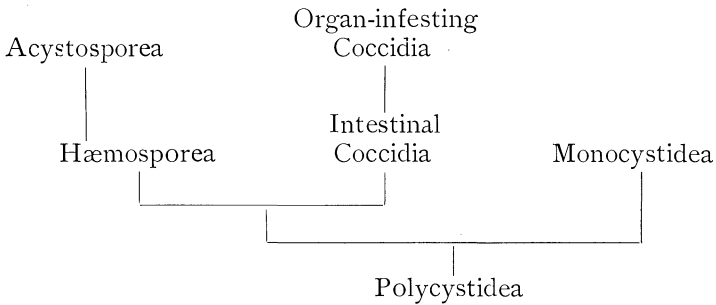
² *Zööl. Jahrb., Abth. f. Anat.*, vol. 15, 1902, pt. 4, p. 693.

evolution when the Acystosporea could infect their vertebrate hosts in two ways, but the intestinal method is now lost. The acquisition of an intermediate host is obviously advantageous to the species, tending, as it does, to a wider distribution.

There are, however, anatomical differences between the Hæmosporea and the Acystosporea. The former, in the trophozoite stage, possess a definite body form, on which account they are often spoken of as Hæmogregarines. This definite form is due to the presence of a dense hyaline ectosarc, in which myocyte fibrillæ have been demonstrated. These animals, although typically cell parasites, indulge in frequent migrations in the blood plasma, and during such "free" phases, they display both contractile and locomotor movements. On the other hand, the trophozoites of the Acystosporea appear never to migrate. The blood cell originally attacked is abandoned only after the organism has divided by schizogony. No special anatomical differentiation appears to have been described, but the trophozoites undergo sluggish amœboid movements. Accordingly, as regards both the morphology and the life history, the Acystosporea are clearly the more specialized group. It next remains to relate the blood parasites with their closest relatives, the Coccidia.

As regards the life history, the parallelism is exact, except for the acquisition of an intermediate host in the Acystosporea. The sexual processes are practically identical. Morphologically, however, the Coccidia are practically on a par with the Acystosporea and considerably more degraded than the Hæmosporea. Comparing the Coccidia and the Hæmosporea, the former would, according to our criteria, be the derived group. But the favored habitat of the Coccidia is the epithelium of the intestine, and it seems as if this must have been occupied by Sporozoan parasites before invasion of the blood.

The view advanced by Minchin seems best to fit the case. This is that both Coccidia and Hæmosporidia have arisen from common ancestors. These ancestors in their turn I believe to have been derived from the Polycystidea, and my conception of the interrelationships of the Telosporidia is indicated by the following scheme : —



The habitat of the Polycystidea, the intestine of their hosts, has enabled them to lead a practically free life. Accordingly, they are the least modified of all Sporozoa, and have retained nearly as complex an organization as the Flagellates. They have given rise, on the one side, to the Monocystidea and on the other to the Coccidiomorpha. The former followed much the same lines as their immediate ancestors, but have undergone morphological degradation. The Coccidiomorpha became adapted to an intracellular life, and separated into two groups. In one of these, the inert Coccidia, morphological degradation has been carried to its extreme. The greater anatomical complexity of the Hæmosporea is to be credited to their habitat. The liquid blood offers a radically different environment from the motionless epithelium. In consequence, the power to move, possessed at the outset by the Hæmosporea as an inheritance from their Polycystid ancestors, has not been lost. Thus these animals possess the characteristic Telosporidian organ of movement, a myocyte. The Acystosporidia, further evolved, have apparently lost the ability to move from place to place. Their inertness, although comparable to that of the Coccidia, has been independently acquired. Finally, in their ability to display amœboid movements, they have not sunk quite so low.

Mesnil¹ considers the ancestral Telosporidian to be a Montocystid intestinal gregarine. Minchin derives the group from a hypothetical intracellular form. In both cases this ancestor is supposed to have given rise to existing gregarines on the one hand, and to the Coccidiomorpha on the other. To my mind,

¹ *Vol. Jubil. Soc. de Biol., Paris, 1899.*

these hypotheses are open to objection in that they are based almost exclusively on the reproductive phenomena. They both involve the evolution of a more from a less complexly organized parasite. I have endeavored to show that this is contrary to what experience teaches us to expect. In our classification of the Metazoa morphology is given first place and it should not be neglected in a consideration of the Protozoa. The remarkable character of the reproductive phenomena displayed by the Sporozoa has, I think, given them an undue importance. The form of the adult animals has, in any attempt at a classification, at least equal value.

We have now to consider the Neosporidia. This subclass is but poorly known. As shown above, it consists of three orders, the Myxosporidia, the Sarcosporidia, and the Haplosporidia. The Myxosporidia are characterized by their peculiar spores, which bear a close resemblance to the stinging cells of coelenterates. The spore consists of a bivalved shell, inclosing the sporoplasm and the polar capsules. The polar capsules, of which there may be from one to four, are tightly coiled filaments which occupy vacuities in the spore substance. Acted upon by the digestive juices of the host, the spore shell opens and the filaments are everted. By means of these filaments the spore is held attached to the intestinal epithelium of the host, and the sporoplasm escapes as a minute amœbula. Freed on the surface of a host cell, it works its way within and comes to rest. The nucleus presently divides, then the cytoplasm, and each spore thus produces a number of bodies which are at least the analogues of the Coccidian merozoites. They scatter throughout the host and each gives origin to a trophozoite. The trophozoite grows larger, becomes multinucleate and soon begins to form spores. These, eventually reaching the exterior, are fitted to infect new hosts.

The above outline of the life history is that given by Doflein. It is to be observed that there is no sexual process. Doflein, however, considers it possible that either the spores themselves may conjugate very shortly after their escape from the spore shell, or else that this process may take place between the young trophozoites. This he advances merely as a surmise, there being no observational evidence.

The young trophozoite may follow one of several lines of development. These lines diverge considerably. The nature of the forms so produced is indicated in the following table, which is taken from Doflein : —

Group I. Free-living forms.

Group II. Sedentary forms.

1. Inclosed in cysts.
2. In the state of "diffuse infiltration."
3. Cell parasites.

Group I contains the most highly organized of the Myxosporidia. Its members lead a free life in the gall bladder, urinary bladder, or kidney tubules of their hosts. They display differentiation into ectosarc and endosarc. The latter is essentially like that of other Sporozoa. The former is a clear granular layer. It is the seat of motion and gives origin to the pseudopodia. A myocyte does not appear to have been described. Throughout these animals resemble the Rhizopoda.

Group II is doubtless an offshoot from Group I, with the exception of the cell parasites. The encysted forms are those which come to rest at some point within the host's body. The part thus attacked reacts by the formation of a wall around the parasite, which is thereupon prevented from extending its explorations. "Diffuse infiltration" results when the parasite spreads out through a considerable region of the host's tissues. In such cases no cyst is formed. Eventually, these two kinds of trophozoites die as trophozoites, but leave the tissues which they had occupied, filled with spores.

The forms hitherto considered are mostly animals of considerable size, while the cell parasites, which belong to the suborder Cryptocystes, are amongst the smallest of the Sporozoa. The mode of life is, however, much the same. It is to this group that belongs the destructive *Nosema (Glugea) bombycis*, the cause of the silk-worm disease.

In no Myxosporidian is an intermediate host known, and infection is apparently always the result of chance. In those forms which live in such places as the gall or urinary bladder, the

spores are assumed to reach the exterior with the evacuations of the host. For the tissue-infesting species, however, there are no natural channels. Where the parts attached are superficial, it is conceivable that the tumors which so frequently occur in Myxosporidian infection may break to the exterior. In this way the spores would be set free. But in deep-seated infections the conclusion seems inevitable that the death of the host is necessary. This conclusion is supported by the fact that extensive infections are generally fatal.

The Myxosporidia attack cold-blooded vertebrates and arthropods. The Sarcosporidia confine their attentions to birds and mammals. They are very abundant in the visceral muscles of sheep and swine. While their spores differ from those of the Myxosporidia, the animals themselves are morphologically a good deal like those members of the last-named group which live in cysts or in the state of diffuse infiltration. Additional data regarding them are a crying need and at present all that can be said is that they have probably evolved from Myxosporidian-like ancestors. The Haplosporidia may be dismissed at once. Our knowledge is too scanty to warrant any generalizations.

It is possible, however, to compare the Neosporidia with the Telosporidia. Taking the free-living Myxosporidia on the one hand, and the Polycystidea on the other, we fail to detect any points of similarity. The habitats, life histories, and reproductive processes are wholly different. There is no morphological likeness in any of the stages, from spore to trophozoite. In a few cases, gregarines are almost amœboid and can protrude pseudopodia. The Monocystids, also, are coelomic parasites and some species live in the organic cavities of their hosts. But this appears to be the sum total of the evidence indicative of any connection between the two groups. It is palpably insufficient.

Unless, then, future discoveries of a fundamental nature shall be made, there seems ample warrant for the view expressed by Mesnil and Doflein. This is that the Telosporidia and Neosporidia are not genetically connected. Accordingly, at least for the present, we should use the term Sporozoa merely as a convenient cloak. It serves to cover certain Protozoa which cannot be placed in any of the other Protozoan classes. It is not so long

since the so called Vermes subserved a like function among the invertebrates. Happily, in this case, confusion has been reduced to order and we who are interested in the Protozoa may hope that history will repeat itself.

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